SKELETAL PARTS OF THE STING APPARATUS OF SELECTED SPECIES IN THE FAMILY ANDRENIDAE (APOIDEA: HYMENOPTERA)

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Abstract.—The morphological structure of the skeletal parts of the sting apparatus for five species in the family Andrenidae are described. The sting apparatus is well-developed, even though a previous study reported that some of the species studied lack a sting.

It is well established that the females of Apoidea (Hymenoptera) have a sting apparatus the function of which is for individual or social protection (Michener, 1974). In fact, the sting apparatus of Apoidea is a highly modified ovipositor, which has completely lost its original and primary egg laying function since the eggs are laid directly from the genital chamber.

The sting apparatus is composed of two basic and functionally different parts: (1) Skeletal parts and muscles, used to penetrate into the body of the victim and to inject venom; and (2) glands (venom gland, Dufour's gland, Koshewnikow's gland) which have different functions. The largest sting gland is the venom gland, and it produces the venom (Oeser, 1961; Maschwitz and Kloft, 1971; Rathmayer, 1978). For the function of Dufour's gland, there are many speculations (see Maschwitz and Kloft, 1971). In primitive bees Dufour's gland produces a waterproof membrane for lining the nest cells (Lello, 1971a). In species of Apidae that build nest cells from resin or produce wax, Dufour's gland functions to protect the eggs and hold them in the cells (Lello, 1976). Koshewnikow's gland, found in workers and queens of *Apis*, secretes the alarm substance (Maschwitz and Kloft, 1971).

Although the sting apparatus of Apoidea has been studied by many authors (e.g. Snodgrass, 1935, 1956; D'Rozario, 1940; Oeser, 1961; Robertson, 1968; Maschwitz and Kloft, 1971; Matsuda, 1976; Radović, 1976; Richards, 1977; Rathmayer, 1978; Kugler, 1978; and Evans et al., 1979), much remains to be learned. Among aculeate Hymenoptera the skeletal parts of the sting apparatus have been studied the most and are comparatively well known

VOLUME 82, NUMBER 4

for the genera *Apis* and *Vespa*. This apparatus has been studied from several different aspects including morphological, histological, physiological, and biochemical. The anatomy and histology of the glandular parts of the sting apparatus of Apoidea were studied by Lello (1971a–d, 1976).

In her studies Lello (1971a) stated that Andrena (Parandrena) andrenoides (Cresson) and Andrena (Tylandrena) erythrogaster (Ashmead) "lack the sting apparatus," and that the sting apparatus is lacking among representatives of the family Andrenidae. Michener (1974) stated that the sting apparatus is reduced and functionless among most Andrenidae. However, our intensive anatomical study of the skeletal parts of the sting apparatus of Sphecoidea and Apoidea show that the sting is present and well-developed in the investigated representatives of Andrenidae; moreover, skeletal parts of the sting apparatus have been discovered in species that are supposed to lack them.

MATERIALS AND METHODS

We studied five North American species of the family Andrenidae: Andrena (Calandrena) accepta Viereck from Virginia, Andrena (Parandrena) andrenoides (Cresson) from Colorado, Andrena (Tylandrena) erythrogaster (Ashmead) from Indiana (Andreninae); and Protandrena bancrofti Dunning from Nebraska, and Perdita (Perdita) indioensis Timberlake from California (Pangurinae). The classification of Apoidea as presented by Hurd (1979) is used in this study.

Dried skeletal parts of the sting apparatus were studied. Specimens were softened by soaking them in a jar humidifier for 48 hours. Dissection was performed in 70% ethyl alcohol under a binocular microscope and the dissected sting apparatus was immersed in a solution (lactic acid, glycerin, 40% formaldehyde; 10.0:2.0:0.4 ccm) for 2–3 days to clear the chitinous parts. Clearing the sting apparatus in KOH proved unsatisfactory because sensitive and fine structures, especially Valvulae III (sting sheath), were destroyed. In order to dehydrate, the sting apparatus was taken through a series of ethyl alcohol of increasing concentrations then placed into xylol, and, in the final step, the skeletal parts of the sting were placed in a drop of Canada balsam on microscope slides. The illustrations were made by use of the Bausch and Lomb Tri-Simplex microprojector.

RESULTS AND DISCUSSION

The skeletal parts of the five species studied are in fact modified parts of the 8th and 9th abdominal segments.

The shaft of the sting ("the sting" used in the narrower sense of the word) is composed of two pairs of valvulae: vavulae II and valvulae I. Valvulae II is derived from skeletal elements of the 9th abdominal segment. This pair

of valvulae is linked together in such a way that at the base they form the bulbus (sting bulbus), while the distal part is prolonged, thus forming the stylet (sting stylet). The channels of the venom and Dufour's sting glands empty inside the sting bulbus. From the lower part of valvulae II there is a pair of valvulae I or lancets. Valvulae I are prolonged, free skeletal parts, which form a channel through which the venom from the bulbus is ejected. Valvulae I (lancets) are skeletal elements of the 8th abdominal segment.

From the basal part of each of valvulae I originates their rami (Ramus I) which look like thin, bent, skeletal elements in the form of an arch. At their distal ends the rami merge into the triangular skeletal parts, which, because of their shape, are called triangular plates (valvifer I). It is believed that the triangular plates are an addition (a growth) to the base of valvulae I and, according to their origin, are remnants of the reduced and membranous sternum of the 8th abdominal segment.

From the basal part of valvulae II, i.e. from the sting bulbus, extend the rami (ramus II), which are thin and arched. They stretch along rami I. At the distal end rami II are connected with the oblong, widened and arched skeletal elements and are termed oblongate plates or valvifer II. Oblongate plates are remnants of the 9th abdominal sternum.

In addition to the two pairs of valvulae (valvulae I and valvulae II), the sting apparatus consists of another pair of valvulae (valvulae III), which are designated as the sting palpus or sheath. Valvulae III cover the stylet when in resting position, i.e. they somewhat form a cover. Valvulae III are rather wide and on the outside areas are covered with sensory bristles, the number of which is especially numerous distally. These sensory bristles are in fact sensory parts of the sting apparatus which first come in contact with the body of the victim. When incited they activate the stylet, and this is followed by the stinging act (Snodgrass, 1956). Valvulae III are modified skeletal parts of the 9th abdominal segment.

In addition to the above-mentioned, the sting apparatus contains a pair of quadrate plates which were derived from the 9th abdominal tergum and are divided into two hemitergites. Quadrate plates are relatively large skeletal parts, and they partially cover the oblongate plates.

The sting apparatus also has a membranous middle part of the 9th abdominal sternum which is folded over the base of the sting and is usually provided with setae on its apical part. The shape and the structure of the sting apparatus of the analyzed species are as illustrated (Figs. 1–5). Characteristic features of these species may be summarized as follows:

The sting apparatus of *Andrena (Callandrena) accepta* possesses a welldeveloped and prolonged stylet and lancets. Valvulae III are somewhat shorter. The oblongate and quadrate plates are more elongate than those of other species studied.

VOLUME 82, NUMBER 4



Figs. 1–5. Sting apparatus. 1, Andrena (Callandrena) accepta. 2, A. (Parandrena) and drenoides. 3, A. (Tylandrena) erythrogaster. 4, Protandrena bancrafti. 5, Perdita (Perdita) indioensis. 1–3, 5, dorsal view. 4, lateral view.

In Andrena (Parandrena) and renoides and Andrena (Tylandrena) erythrogaster, which Lello stated lack a sting, the sting apparatus is present and is somewhat wider compared with A. (C.) accepta. The stylet and lancets of A. (P.) and renoides are considerably shorter than those of A. (*T.*) erythrogaster. The quadrate plates are very large and cover the greater part of the lateral areas of the sting apparatus. Valvulae III are well-developed, broadened, and composed of only one piece. They are covered with many thick and long sensory bristles. The sting apparatus of *A*. (*T*.) erythrogaster is similar in shape to that of *A*. (*P*.) andrenoides; however, the quadrate plates are shorter and differ in their more elongate shape; valvulae III are thickened, well-developed, and are almost the same length as the sting; and there are fewer sensory bristles than in previously mentioned species. In addition to the differences in shape, *A*. (*P*.) andrenoides and *A*. (*T*.) erythrogaster possess in common a rather large and well-developed sting bulbus.

In *Protandrena bancrofti* the stylet and lancets are long and distinct. The quadrate plates are well-developed as well and valvulae III are considerably shorter than the stylet and are covered with sensory bristles.

The sting apparatus of *Perdita* (*Perdita*) *indioensis* is similarly well-developed. The stylet is elongated. Valvulae III are somewhat shorter than the stylet and have a rather prolonged shape compared with the afore-mentioned species.

CONCLUSIONS

A study of the structure of the skeletal parts of the sting apparatus for five selected species of Andrenidae reveals the following:

(1) A sting apparatus, characteristic of aculeate Hymenoptera, is present in the representatives of this family, despite the conclusion by Lello that Andrenidae lack a sting.

(2) All skeletal parts of the sting apparatus of aculeate Hymenoptera are present in the analyzed species.

(3) Each of the species studied has a characteristic (specific) shape of skeletal parts composing the sting apparatus.

(4) The greatest similarity in the structure of the skeletal parts of the sting apparatus among the analyzed species is between *Andrena (Parandrena) andrenoides* and *Andrena (Tylandrena) erythrogaster*. Even so, each of the studied species exhibits certain specific differences in the structure of separate skeletal parts.

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LITERATURE CITED

- Evans, H. E., C. Kugler, and W. I. Brown, Jr. 1979. Rediscovery of *Scolebythus madecassus* with a description of the male and the female sting apparatus (Hymenoptera: Scolebythidae). Psyche (Camb. Mass.) 86: 45–51.
- Hurd, P. D., Jr. 1979. Superfamily Apoidea, pp. 1741–2209. In Krombein, K. V. et al., eds., Catalog of Hymenoptera in America North of Mexico, V. 2. Smithsonian Institution Press, Washington, D.C.
- Kugler, C. 1978. A comparative study of the Myrmicinae sting apparatus (Hymenoptera, Formicidae). Studia Entomol. 20: 413–548.
- Lello, E. 1971a. Adnexal glands of the sting apparatus of the bees: Anatomy and histology 1 (Hymenoptera: Colletidae and Andrenidae). J. Kans. Entomol. Soc. 44: 5-13.
- . 1971c. Anatomia e histologia das glândulas do ferrão das abelhas. III (Hymenoptera: Megachilidae e Melittidae). Cienc. Cult. (São Paulo) 23: 243–258.
- ———, 1976. Adnexal glands of the sting apparatus in bees: Anatomy and histology, V (Hymenoptera: Apidae), J. Kans. Entomol. Soc. 49: 85–99.
- Maschwitz, U. and W. Kloft. 1971. Morphology and function of the venom apparatus of insects—bees, wasps, ants and caterpillars. In W. Buchler and E. E. Buckley, eds., Venomous Animals and Their Venoms, Vol. III. Academic Press, New York.
- Matsuda, R. 1976. Morphology and Evolution of the Insect Abdomen. Pergamon Press Inc., New York, 534 pp.
- Michener, C. D. 1974. The Social Behavior of the Bees: A Comparative Study. The Belknap Press of Harvard University Press, Cambridge, Massachusetts. 404 pp.
- Oeser, R. 1961. Vergleichend-morphologische Untersuchungen uber den Ovipositor der Hymenopteren. Mitt. Zool. Mus. Berl. 37: 3-119.
- Radović, I. 1976. Morphological characteristics of living form of digger-wasps (Sphecidae) with the special regard on adaptive change of fore leg structure and sting. Unpublished M.S. thesis, Faculty of Science, University of Belgrade, pp. 1–120, figs. 1–149.
- Rathmayer, W. 1978. Venoms of Sphecidae, Pompilidae, Mutillidae and Bethylidae. In Bettini, S., ed., Handbook of Experimental Pharmacology, Vol. 48, Arthropod Venoms, Heidelberg and New York.
- Richards, O. W. 1977. Hymenoptera. Introduction and key to families. Handb. Ident. Br. Insects, R. Entomol. Soc. Lond. 6(1): 1–100.
- Robertson, P. L. 1968. A morphological and functional study of the venom apparatus in representatives of some major groups of Hymenoptera. Aust. J. Zool. 16: 133–166.
- D'Rozario, A. M. 1940. On the development and homologies of the genitalia and their ducts in Hymenoptera. Trans. R. Entomol. Soc. Lond. 92: 363–415.
- Snodgrass, R. E. 1935. Principles of Insect Morphology. McGraw-Hill Book Company, New York and London. 667 pp.
- . 1956. Anatomy of the honey bee. Comstock Publ. Assoc. Cornell Univ. Press, Ithaca, New York, 334 pp.